Molluscan Faunas of Pacific Coast Salt Marshes and Tidal Creeks

BY

KEITH B. MACDONALD [1]

Scripps Institution of Oceanography, La Jolla, California 92037

(1 Map)

INTRODUCTION

Pacific Coast *Spartina* - *Salicornia* salt marshes, and the tidal creeks that dissect them, contain distinctive molluscan faunas. The taxonomy of most of the species represented in these faunas is well documented (Fitch, 1953; Palmer, 1958; Keen, 1958, 1963; Hanna, 1966) and in some cases papers describing aspects of the ecology of individual species, or of closely related species in other localities are available (e. g., Hauseman, 1932; MacGinitie, 1935; Sander, 1950; Yonge, 1951; Meyer, 1955; Sellmer, 1967).

These faunas deserve further study, not only because they occupy habitats that are rapidly disappearing on the Pacific Coast, but because the huge species populations found at several sites may play an important role in the cycling of nutrients and detritus (organic debris) and thus indirectly affect offshore communities (Newell, 1965; Carriker, 1967; Hedgpeth, 1967).

This report outlines the geographic distribution and relative abundance of the species represented in these faunas. No previous studies of this subject have been found in the literature.

METHODS

Salt marshes and tidal creeks in 9 Pacific Coast bays and estuaries were examined (Figure 1). At 7 of these localities single sites were sampled. Local spacial variations were studied by sampling 2 sites at both Tomales Bay and San Quintín Bay. Ten of the sites were sampled only once, each sample-set being collected over a 2 - 3 day period. To provide a basis for separating real latitudinal differences from yearly population fluctuations, 5 replicate sample-sets were taken at Mission Bay, at approximately quarterly intervals (November 1964 to July 1966).

Individual sites were selected for a minimum of pollution and freshwater runoff. Isolated marshes that could be sampled as discreet units were preferred to artificially defined sections of more extensive marshlands.

At each site the vegetated marsh surfaces and tidal creeks were sampled independently. For the former, stratified random sampling patterns were set up (Cochran, 1954). Random number tables were used either to locate samples at random intervals paced along previously surveyed relief transects, or, to select pairs of random coordinates locating the samples within quadrants of a prescribed irregular area. The molluscan data were collected from stainless steel rings enclosing an area of 200 cm^2; each sample was excavated to a depth of 1 cm.

At 9 of the sites the tidal creek samples were located at random intervals paced along the creek banks; at Grays Harbor and Mission Bay these samples were collected at fixed intervals. In most cases (cf. Table 2) the creek bottom mollusks were sampled from 25 × 25 cm quadrats excavated to a depth of approximately 25 cm. Upon return to the laboratory each marsh or creek sample was washed through a 1 mm mesh screen and all of its molluscan components were sorted, identified and counted (see Macdonald, 1967, for additional details of sites and sampling methods).

RESULTS AND DISCUSSION

Seventy-six mollusk species were collected during this study; 64 of these were represented in the quantitative samples and the remainder were picked up during reconnaissance of the sites. In the samples, 2 species were represented by live specimens only, 28 species by both

[1] Present address: Department of Geology, University of California, Santa Barbara, California 93106

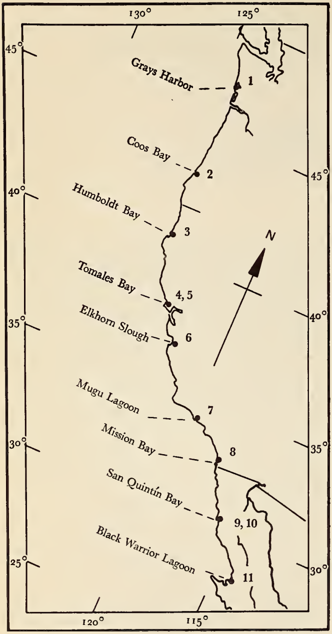

Figure 1

North American Pacific Coast, showing the general location of the sites investigated

living and dead material and the remaining 34 species by empty shells only. Only the live material from the quantitative samples is considered in this report.

The geographic distribution and relative abundance (i. e., percentage of total individuals, per sample set) of the mollusks represented in the live material are shown in Tables 1 and 2. Table 3 summarizes seasonal changes in the relative abundance of selected species in the replicate samples taken at Mission Bay.

ABUNDANCE

In sets of 25 - 178 samples, 2 - 7 species were found in the salt marshes and from 0 - 11 in the tidal creeks. The number of species increases significantly southward in the marsh environment (Kendall rank correlation procedure, $P < 0.05$, 1-tailed). There is similar increase in the tidal creeks, but largely because of the poor representation of mollusks at San Quintín Bay (Keen, 1962), it is not significant ($P > 0.05$).

The mean density of mollusks (i. e., total individuals per sample set/combined area of samples) and the mean densities of separate species in both environments show no correlation with the number of species recorded from each marsh or creek, or with the latitude or area of the site being sampled. This suggests that the abundance of mollusks at a specific site is controlled by a variety of local factors (sediment type, food supply, etc.) rather than by regional trends of climatic or oceanographic variables.

The distribution of individuals between species exhibits a distinct pattern in the faunas of both environments: 90 - 100% of the individuals collected in each sample set belonged to 2 or 3 species; any additional species present were each represented by relatively very small numbers of individuals. Inspection of individual sample-sets also reveals that the abundant species were widely distributed at each site whereas the less common species had markedly patchy distributions. This pattern remains essentially the same despite differences in the latitude and area of the site and the species compositon and density of the faunas.

SPECIES COMPOSITION

The creek faunas usually contain more species and have a more variable species composition than do those of the marshes. In part this may reflect the more highly specialized fauna of the latter, a marked contrast to that of the less extreme creek environments which contain a wide variety of species found in other barely subtidal habitats. Since a majority (83%) of the creek species are infaunal and thus subject to the selective effects of substrate (Thorson, 1957; Purdy, 1964) the compositional variability between sites might also reflect the variable nature of creek sediments. For example, at Tomales Bay shelly

Table 1

Salt Marsh Mollusk Faunas
Species Composition and Relative Abundance (i. e., percentage of total individuals per site)

	Locality[1]										
Species	1	2	3	4	5	6	7	8[A]	9	10	11
Gastropoda											
Littorina newcombiana (Hemphill, 1876)	90.6	52.3	0.3								
Phytia myosotis (Draparnaud, 1801)	**	3.7	65.8	64.1	7.1	45.0					
Assiminea translucens (Carpenter, 1864)	9.4	44.0	33.9	35.9	8.8	55.0	93.2	68.6	79.3	76.0	5.0
Batillaria zonalis (Bruguière, 1792) †					84.1						
Cerithidea californica (Haldeman, 1840)					*		5.9	28.2	20.0	17.1	34.5
Melampus olivaceus Carpenter, 1857							0.8	0.9	*	0.3	32.4
Littorina scutulata Gould, 1849							+	+			
Acteocina culcitella (Gould, 1852)								2.0	0.7	5.5	
Littorina planaxis (Philippi, 1847)								+			
Acteocina carinata (Carpenter, 1857)											27.6
Bivalvia											
Chione fluctifraga (Sowerby, 1853)								+			0.5
Mytilus edulis Linnaeus, 1758								*			
Ostrea lurida Carpenter, 1864								*			
Lasaea subviridis Dall, 1899										1.1	
Total individuals	553	300	693	245	309	5246	2282	2153	852	362	809
Marsh area (km^2)	0.237	0.071	0.056	0.111	0.046	0.104	0.886	0.139	0.060	0.019	0.099
Number of samples	50	59	40	49	20	45	60	100	50	20	50

[1] Localities as in Figure 1
+ = present, < 0.1% individuals per site
* = present at site but did not occur in samples
† = introduced species, not native to the West Coast
** = common at other sites around Grays Harbor
[A] Mission Bay values obtained from combined replicate sample sets

gravels were common, at Grays Harbor only coarse clean sands were present, at Coos Bay both soft muds rich in plant debris and firmer muddy sands were found and at the Humboldt Bay and San Quintín Bay sites almost liquid muds predominated.

The geographic distribution of recurrent groups of species supports the classification of Pacific Coast molluscan provinces proposed by Valentine (1966). Within the salt marsh faunas the Californian (27° - 34° N) and Oregonian (34° - 50° N) provinces are characterized by *Assiminea - Cerithidea* and *Assiminea - Phytia* associations respectively.

The distribution of the more abundant tidal creek species suggests that the Oregonian Province can be further divided into 2 sub-provinces: the *Macoma - Mya* assemblage from Grays Harbor and Coos Bay, and represented by *in situ* empty shells at Humboldt Bay, characterizing a northern sub-province; the *Batillaria - Gemma* (both introduced species) assemblage from Tomales Bay and Elkhorn Slough characterizing a southern one. The *Acteocina - Cerithidea* association found in the tidal creeks south of Point Conception characterizes the Californian Province.

LOCAL VARIATION

Reconnaissance of different sites bordering the same bay or estuary indicates that the faunas of adjacent marshes or creek systems can vary considerably. Some of this variation reflects the environmental gradients characteristic of estuaries: for example, *Phytia myosotis* was not found at Westport but was common at other sites well within Grays Harbor (Markham, Oyhut), perhaps indicating a preference for less exposed or more brackish habitats. Conversely, *Littorina newcombiana* was very rare at Arcata but reached densities of 16 to 48 per m^2 on Samoa Marsh near the mouth of Humboldt Bay, suggesting a

Table 2

Tidal Creek Mollusk Faunas: Species Composition and Relative Abundance

Species	Locality[1] 1	2	3	4	5	6	7	8[A]	9	10	11
Gastropoda											
Littorina newcombiana (Hemphill, 1876)	0.7										
Batillaria zonalis (Bruguière, 1792) †				92.2	63.9	43.0					
Assiminea translucens (Carpenter, 1864)					0.1			+			
Cerithidea californica (Haldeman, 1840)					*		84.4	28.2	3.5	78.0	74.4
Acteocina culcitella (Gould, 1852)							11.5	68.7	29.4	22.0	
Bulla gouldiana Pilsbry, 1893							0.1	+			
Siphonaria brannani Stearns, 1873								+			
Nassarius tegula (Reeve, 1853)								1.4			4.4[E]
Bittium sp.									67.1		
Acteocina carinata (Carpenter, 1857)											19.4
Bivalvia											
Macoma inconspicua (Broderip & Sowerby, 1829)	77.5	7.2									
Mya arenaria Linnaeus, 1758	4.2	71.4			0.1						
Cryptomya californica (Conrad, 1837)	1.4				0.1			*			
Macoma nasuta (Conrad, 1837)	16.2					+	0.6	*			
Laternula japonica (Lischke, 1872) †		21.4									
Gemma gemma (Totten, 1834) †				7.8	29.7	56.9					
Modiolus senhousei (Benson, 1842) †					5.3	*		0.6			
Protothaca staminea (Conrad, 1837)					0.6		2.8	0.2			
Tapes japonica Deshayes, 1853 †					0.1						
Mytilus edulis Linnaeus, 1758						+	0.1	*			
Chione undatella (Sowerby, 1835)							0.4	*			
Lyonsia gouldii Dall, 1915								+			
Chione fluctifraga (Sowerby, 1853)								0.6			1.3
Tagelus californianus (Conrad, 1837)								0.3			0.4
Total individuals	142	14	0	490	1010	3179	720	5462	681	1496	227
Creek area (km^2)	0.026	0.006	0.003	0.008	0.004	0.004	0.045	0.003	0.003	0.001	0.003
Number of samples	20	29	16	18[B]	5[C]	20[D]	15	78	10	4	10

[1] Localities as in Figure 1

For explanation of symbols, see Table 1

[B]: sample size 312 cm^2; [C]: sample size 400 cm^2; [D]: sample size 200 cm^2; [E]: represented by *Nassarius tegula tiarula* (Kiener, 1834), a possible subspecies.

Table 3

Mission Bay
Relative abundance of selected species in successive sample sets

	A	B	C	D	E
Salt marsh					
Assiminea translucens (CARPENTER, 1864)		58.6	59.5	58.2	80.2
Cerithidea californica (HALDEMAN, 1840)		36.4	32.9	41.1	19.1
Acteocina culcitella (GOULD, 1852)		0	7.2	0.7	0.3
Melampus olivaceus CARPENTER, 1857		4.9	0	0	0.2
Tidal creek					
Acteocina culcitella (CARPENTER, 1864)	77.0	45.7	66.5	85.4	61.1
Cerithidea californica (HALDEMAN, 1840)	19.9	50.0	30.4	13.0	35.9
Nassarius tegula (REEVE, 1853)	1.8	2.1	0.2	0.2	1.4

[A] = November 1964 (marsh samples hand-picked in the field, data found unreliable)
[B] = July 1965; [C] = October 1965; [D] = March 1966;
[E] = July 1966

preference for less brackish environments.

Data from Tomales Bay and San Quintín Bay suggest that differences of drainage pattern, substrate or vegetation can also account for local variability. The dominance of *Bittium* in the creek fauna of one of the San Quintín sites (10), for example, reflects the presence of dense *Zostera* (Eel-grass) beds, absent from the other site (9). Similarly, much of Millerton's (5) diverse fauna was collected from a network of narrow protected creeks with soft mud bottoms, while at Walker Creek (4) exposed, deep-water creeks with gravel bottoms were sampled. Possibly the highly dissected nature of the Millerton marsh also allowed *Batillaria* to remain closer to water sources and successfully colonize the marsh surface while it did not do so at either Walker Creek or Moss Landing (6).

SEASONALITY

Data from replicate samples taken at Mission Bay (Table 3) suggest that the relative proportions of the more abundant species remain generally similar throughout the year. Changes noted among the less common species probably reflect the sampling problems associated with rare or accidental species (e. g., *Bulla gouldiana, Littorina planaxis, Siphonaria brannani*), or with patchily distributed species (e. g., Index of Dispersion indicated that all the bivalve species were aggregated), rather than real compositional differences.

Seasonality was noted in *Melampus olivaceus* and *Nassarius tegula*. The former exhibited hibernation behavior similar to that described in *M. bidentatus* (HAUSEMAN, 1932) and was generally absent from the marsh surface from about November through March. During this period many individuals were found clustered together in crab burrows 5 - 10 cm beneath the surface. *Nassarius* appeared to be a seasonal migrant into creek habitats rather than a permanent resident; January, March and October samples showed individuals to be restricted to the creek mouth, while in July they extended well upstream. The apparent seasonality of *Acteocina* in the marsh fauna marked the establishment of small temporary populations from larvae accidentally washed ashore.

Several new species records and range extensions have been noted during this study. For example, *Laternula* is not a native West Coast genus and the occurrence of *Laternula* sp., cf. *L. japonica* (LISCHKE) at Pony Slough, Coos Bay, Oregon, is the first known record of this species from the North American Pacific Coast. Occurrences of *Modiolus senhousei* (BENSON) at Elkhorn Slough and Mission Bay represent a considerable southward extension of the previously known West Coast range (36° to 48° N, HANNA, 1966) of this introduced species. The occurrence at Mission Bay of *Siphonaria brannani* STEARNS, previously known only from a single site near Santa Barbara (≈34° N; KEEN, 1937), also represents a range extension. Several of the salt marsh gastropods, *Assiminea translucens* (CARPENTER), *Phytia myosotis* (DRAPARNAUD) and *Littorina newcombiana* (HEMPHILL) were previously known only from scattered localities (TRYON, 1865; HEMPHILL, 1876; BARTSCH, 1920; PAULSON, 1957; DUGGAN, 1965; HANNA, 1966); this study indicates that in fact these species are widely distributed on most marine marshes between latitudes 25° to 48° N, 35° to 49° N, and 41° to 47° N, respectively.

SUMMARY

Quantitative sampling at 11 sites between latitudes 27° to 48° N reveals that the molluscan faunas of Pacific Coast salt marshes and tidal creeks have a characteristic structure. At each site one or two species are widely distributed and very abundant; additional species are all represented by small numbers of very patchily distributed individuals. The creek faunas usually contain more species and have a more variable species composition than do the marsh faunas.

The geographic distribution of recurrent species groups supports the classification of Pacific Coast molluscan provinces proposed by VALENTINE (1966). There are some indications that both environments in the Californian Province (27° - 34° N) contain a greater variety of species than do similar environments in the Oregonian Province (34° - 50° N).

Now that the general composition of these faunas is known, their community interrelationships and ecological significance can be assessed through experimental studies of their more common species.

ACKNOWLEDGMENTS

Financial support was made available through the Scripps Institution of Oceanography and the United States Steel Research Fund. I wish to thank E. W. Fager for his advice and encouragement throughout this study. Identifications of the molluscan material were confirmed by: E. P. Chace (Natural History Museum, San Diego), A. Myra Keen (Stanford University), R. Stohler (University of California, Berkeley) and D. W. Taylor (U. S. G. S., Menlo Park, California).

LITERATURE CITED

BARTSCH, PAUL
1920. The West American mollusks of the families Rissoellidae and Synceratidae, and the rissoid genus *Barleeia*. Proc. U. S. Nat. Mus. 58 (2331): 159 - 176; plts. 12, 13 (9 November 1920)

CARRIKER, MELBOURNE ROMAINE
1967. Ecology of estuarine benthic invertebrates: A perspective. pp. 442 - 487 *In*: G. H. LAUFF (ed.) Estuaries, Amer. Assoc. Adv. Sci., Washington

COCHRAN, W. A. *et al.*
1954. Principles of sampling. Journ. Amer. Stat. Assoc. 49: 13 - 35

DUGGAN, ELEANOR P.
1963. Report of non-indigenous marine shells collected in the State of Washington. The Veliger 6 (2): 112 (1 October 1963)

FITCH, JOHN EDGAR
1953. Common marine bivalves of California. Calif. Dept. Fish & Game Bull. 90: 102 pp.; illust.

HANNA, G DALLAS
1966. Introduced mollusks of western North America. Occ. Pap. Calif. Acad. Sci. no. 48: 108 pp.; 85 figs.; 4 plts. (16 February 1966)

HAUSEMAN, S. A.
1932. A contribution to the ecology of the salt-marsh snail, *Melampus bidentatus* SAY. Amer. Naturalist 66: 541 - 545

HEDGPETH, JOEL W.
1967. The sense of the meeting. pp. 707 - 710 *In*: G. H. LAUFF (ed.), Estuaries. Amer. Assoc. Adv. Sci., Washington

HEMPHILL, HENRY
1876. Description of a new California mollusc. Proc. Cal. Acad. Sci. 6: 49

KEEN, A. MYRA
1937. An abridged check list and bibliography of west North American marine Mollusca. Stanford Univ. Press, Stanford, Calif.; pp. 1 - 88; 2 figs. (29 September 1937)
1958. Sea shells of tropical West America; marine mollusks from Lower California to Colombia. i - xi + 624 pp.; 10 colored plts.; 1700 text figs. Stanford Univ. Press, Stanford. Calif. (5 December 1958)
1962. A new West Mexican subgenus and new species of Montacutidae (Mollusca, Pelecypoda) ... Pacific Naturalist 3 (9): 321 - 328; 5 text figs. (16 October 1962)
1963. Marine molluscan genera of western North America: an illustrated key. Stanford Univ. Press; 1 - 126; illust.

MACDONALD, KEITH B.
1967. Quantitative studies of salt marsh mollusc faunas from the North American Pacific coast. Univ. Calif., San Diego. Ph. D. Thesis, 291 pp.

MACGINITIE, GEORGE EBER
1935. Ecological aspects of a California marine estuary. Amer. Midl. Natur., 16 (5): 629 - 765

MEYER, K. O.
1955. Naturgeschichte der Strandschnecke *Ovatella myosotis* (DRAPARNAUD). Arch. Molluskenk. 84: 1 - 43

NEWELL, R.
1965. The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. Proc. Zool. Soc. London 144: 25 - 45

PALMER, KATHERINE VAN WINKLE
1958. Type specimens of marine mollusca described by P. P. Carpenter from the West Coast (San Diego to British Columbia). Memoir 76, Geol. Soc. Amer. i - viii + 1 - 376; plts. 1 - 35. New York, N. Y. (8 December 1958)

PAULSON, EDWARD G.
1957. Taxonomy of salt marsh snail, *Ovatella myosotis*, in central California. Nautilus 71 (1): 4 - 7; 1 fig.

PURDY, E. A.
1964. Sediments as substrates. pp. 238 - 271, *In*: J. IMBRIE & N. D. NEWELL (ed.), Approaches to Paleoecology. Wiley,

New York
SANDER, K.
1950. Beobachtungen zur Fortpflanzung von *Assiminea grayana* LEACH. Arch. Molluskenk. 79: 147 - 149
SELLMER, G. P.
1967. Functional morphology and ecological life history of the gem clam, *Gemma gemma*. Malacologia 5: 137 - 223
THORSON, GUNNAR
1957. Bottom communities. *In* Treatise on marine ecology and paleoecology. J. W. Hedgpeth (ed.) Geol. Soc. Amer. Mem. 67, 1: 461 - 534
TRYON, GEORGE WASHINGTON, JR.
1865. Descriptions of new species of *Amnicola, Pomatiopsis, Somatogyrus, Gabbia, Hydrobia* and *Rissoa*. Amer. Journ. Conchology 1: 219 - 222
VALENTINE, JAMES W.
1966. Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf. Limnol. Oceanogr. 11: 198 - 212
YONGE, CHARLES MAURICE
1952. Studies on Pacific coast mollusks. IV. Observation on *Siliqua patula* DIXON and on the evolution within the Solenidae. Univ. Calif. Publ. Zool. 55: 421 - 438.